FOREST HABITAT TYPES OF THE SOUTH WARNER MOUNTAINS, MODOC COUNTY, CALIFORNIA

GREGG M. RIEGEL
U.S.D.A Agricultural Research Service,
920 Valley Road,
Reno, NV 89512

DALE A. THORNBURGH
Department of Forestry, Humboldt State University,
Arcata, CA 95521

JOHN O. SAWYER
Department of Biology, Humboldt State University,
Arcata, CA 95521

ABSTRACT

We describe the forest habitat types of the South Warner Mountains in northeastern California using floristic composition and associated environmental variables from 261 relevés. Floristic data were analyzed with an agglomerative polythetic hierarchical cluster analysis. Results indicate four series (*Cercocarpus ledifolius, Populus tremuloides, Abies concolor,* and *Pinus albicaulis*), containing nine habitat types and two phases. Environmental variables (elevation, aspect, slope, surface rock cover, and topographical position) were ordinated with principal component analysis and a moisture equivalency index. These results indicate that forest habitat types occur along a complex elevation/soil/moisture gradient. The elevation, aspect, and topographic position were the best predictors of general pattern. Only distribution of *Cercocarpus ledifolius* and *Populus tremuloides* series appear to be edaphically controlled.

The montane and subalpine conifer forests of the Warner Mountains in northeastern California are of interest because of their isolation from Sierra Nevada and Cascade Range mountains by the expanses of the Modoc plateau and surrounding deserts (Rundel et al. 1977; Vasek and Thorne 1977). The patchy *Pinus jeffreyi* and *Abies concolor* forests are considered depauperate examples of Sierra Nevada and southern Cascade Range forests (Critchfield and Allenbaugh 1969). Griffin and Critchfield (1972) noted the absence of four montane and subalpine conifers from the Warner Mountains, two that are typically Sierran, *Abies magnifica* and *Pinus lambertiana,* and two that occur in the Pacific Northwest and Sierra Nevada-Cascade Range, *Pseudotsuga menziesii* and *Tsuga mertensiana.* Other investigators have briefly discussed forests that do occur in the Warner Mountains: *Pinus jeffreyi, P. ponderosa,* and *P. washo-*

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ensis forests (Haller 1961, 1965; Pease 1965; Critchfield 1984); *Populus tremuloides* and *Pinus contorta* ssp. *murryana* forests (Vale 1977; Winkler and Dana 1977); and subalpine *P. albicaulis* stands (Critchfield and Allenbaugh 1969; Vale 1977). Classification of forest and range vegetation has been performed in much of the Pacific Northwest and parts of the interior West (e.g., Franklin and Dyrness 1973; Pfister et al. 1977). Pfister and Arno (1980) define habitat type as land areas potentially capable of producing similar climax communities. Mature or near "climax" communities can be identified by the dominant composition of the understory. Since the establishment and development of plants are governed by the environment, specific responses can be expected for an equivalent set of environmental conditions (Daubenmire 1968).

The lack of a habitat type classification in northeastern California and the relatively undisturbed vegetation led us to choose the forests within the South Warner Wilderness Area for our study. Our objective was to describe the habitat types for the forests of the area.

Study Area

We define the South Warner Mountains as the portion of the range south of Cedar Pass (Calif. State Highway 299), and the North Warner Mountains as the portion which is north. The South Warner Wilderness Area of the Modoc National Forest is located between 41°14′ and 41°30′N latitude and 120°07′ and 120°17′W longitude, in the South Warner Mountains of Modoc Co. in the extreme northeastern corner of California. The area encompasses approximately 28,647 ha and averages about 11 km in width and 26 km in length. The Wilderness Area encompasses elevations from 1457 to 3016 m.

Climate is considered continental (Pease 1965). Mean annual precipitation in Jess Valley (1555 m), which is adjacent to the west central portion of the study area, is 454 mm (State of Calif. 1980). The snow pack averages 1077 mm in depth and contains an equivalent 404 mm of water (State of Calif. 1981). Average temperatures in Alturas (1334 m) located 25 km from the study area range from −2.2°C in January to 19.1°C in July (U.S.D.C. Weather Bureau 1970).

The Warner Mountains are part of the western edge of the Great Basin Province. Structurally the range is characteristic of the Great Basin; however, the rocks are compositionally related to the Modoc Plateau (Macdonald and Gay 1966). In general, the rock sequences comprising the Warner Mountains are Miocene volcanic rocks overlying Oligocene sedimentary rocks (Duffield and Weldin 1976). The volcanic rocks consist of rhyolitic ash-flow tuff, andesite flows, rhyolitic to andesitic air-fall pyroclastic deposits, basalt flows or small local rhyolite flows. The sedimentary rocks consist of bedded siltstone and sandstone.

Soils in the study area are classified primarily as mollisols with some alfisols and entisols (Luckow 1986).

Some authorities view the flora of the Warner Mountains to be Sierran (Cronquist et al. 1972; Munz 1973), whereas others consider it more Great Basin or intermountain in character (Raven 1977; Harper et al. 1978; Raven and Axelrod 1978; Reveal 1979). Major and Taylor (1977) have suggested that the presence of Rocky Mountain alpine species found here indicates a floristic, and therefore a probable vegetational, relationship to the east.

Local weather is strongly influenced by the orographic effect of the crest of the South Warner Mountains. The gentle west slope ($\bar{x} = 10°$) receives a greater amount of precipitation than the steeper east slope ($\bar{x} = 25°$), producing extensive forests within a mosaic of sagebrush-steppe and meadows. Vegetation on the east slope is dominated by sagebrush (*Artemisia tridentata*) with scattered forests and meadows associated with drainages and seeps. This general lack of forest may also relate to steep, rocky scarp topography on the east side. Extensive areas of juniper (*Juniperus occidentalis* ssp. *occidentalis*) and sagebrush occur on the lower slopes on both the east and west sides.

The Warner Mountains have served as summer range for livestock since the late 1860's. By 1900, 60,000 sheep and 40,000 cattle were using the Warner Mountains (Pease 1965). In 1904 overgrazing pressures stimulated the formation of a federal reserve to manage the Warner Mountains. The U.S. Forest Service established a primitive area in 1931 which is now the South Warner Wilderness Area. Currently 3000 sheep [1070 AUM's (AUM = animal unit month; cow and calf feed requirement, or equivalent, for one month)] and 120 cattle (396 AUM's) graze in the Wilderness. An additional 402 cattle (1378 AUM's) are on allotments that are partially within the Wilderness boundaries.

Methods

Data collection. Initial reconnaissance occurred in 1978. Sampling was conducted throughout the summers of 1978, 1979, and 1980, with field verification during 1981 and 1983. We did not sample areas with evidence of heavy cattle or sheep grazing (e.g., manure, defoliated plants, and dust wallows). Fire evidence was noted.

Approximately 95% of the forests grow on volcanic soils. Vegetation occurring on sedimentary soil, which typically is conifer woodlands, and the juniper-sagebrush woodlands that occur on the lower slopes of the east side were not sampled. However, undisturbed vegetation outside the wilderness boundary was also examined during the reconnaissance.

Methods were adapted from Mueller-Dombois and Ellenberg (1974), Gauch (1982), and Riegel (1982). Reconnaissance suggested four types of frequently occurring floristic assemblages and associated habitats. Each type was sampled throughout its extent using relevés (Mueller-Dombois and Ellenberg 1974). Sampling was confined to sites possessing a reproducing overstory with consistent aspect and slope. Relevés ranged in size from 8 m^2 to 2000 m^2.

Vascular plant species were censused in the relevé, and each was evaluated in terms of cover and relative abundance using a modified Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974). Average heights of the tree and shrub layers were measured. Diameter at breast height (DBH = 1.37 m) and basal area of trees were measured. Elevation, aspect, slope, topographic position, soil surface texture, surface rock cover, and forest floor depth were measured (Riegel 1982).

A total of 261 relevés contained information of 211 species. Relevé location was recorded on topographic maps deposited in the Archives of Humboldt State University library. Voucher specimens of collected plants are deposited in the Humboldt State University Herbarium (HSC) (Riegel and Schoolcraft 1990). Nomenclature follows Munz (1973).

Data analysis. Agglomerative polythetic hierarchical cluster analysis was used to gain an initial understanding of the structure in the data (Gauch 1982). Relevés were compared using a modified version of Orloci's (1967) similarity coefficient, Euclidean distance (Gauch 1982), and Ward's method (Ward 1963), utilizing error sum of squares. Ward's method was chosen as the cluster technique to create the dendrogram (Riegel 1982). Thirty-five species were very rare and were deleted from the analysis. A summary table was constructed using the groups defined from the interpretation of the dendrogram (Mueller-Dombois and Ellenberg 1974; Gauch 1982) (Table 1).

The classification framework follows Pfister and Arno (1980) using, in increasing order of resolution, 1) *Series* (exhibits major environmental differences reflected by tree distribution and is named for the potentially climax-dominant tree); 2) *Habitat type* (reflects differences in the environment by vegetation composition and is named by the series and characteristic understory species); 3) *Phase* (represents minor environmental differences within a habitat and is named by an indicator species).

Environmental relationships among the groups at both the series and habitat type levels were examined using both direct and indirect gradient analyses. A direct gradient analysis, used elevation, aspect, and topographic position to rate the soil moisture equivalence for each relevé (Sawyer 1975). An indirect technique, principal component analysis was used to derive synthetic environmental axes

TABLE 1. SPECIES PRESENCE (P = percent plots with species) AND MODAL COVER-ABUNDANCE VALUE (C)[a] FOR SPECIES WITH P > 20% IN AT LEAST ONE HABITAT TYPE. [a]1 = one specimen, 2 = sparse, 3 = less than 5%, 4 = 5–25%, 5 = 25–50%, 6 = 50–75%, 7 = 75–100%. [b]*Arnica longifolia, Lupinus polyphyllus,* and *Mimulus guttatus* restricted to type, but of low presence. [c]*Anemone drummondi* restricted to type, but of low presence. [d]The largest P + C for tree canopy, saplings and seedlings presented. See Riegel (1982) for complete differentiated table. [e]As reproduction only.

	(1) POTR/ VECA[b] P/C	(2) POTR/ ASFO P/C	(3) CELA/ BASA P/C	(4) ABCO/ LUCA P/C	(5) PIJE phase P/C	(6) PIWA phase P/C	(7) ABCO/ OSCH P/C	(8) ABCO/ PYPI P/C	(9) PIAL/ STCA P/C	(10) PIAL/ PEGR[c] P/C	(11) PIAL/ ARAC P/C
Trees[d]											
Populus tremuloides	100/4	100/4									
Cerocarpus ledifolius			100/5								
Pinus jeffreyi				65/5	100/5	11/2	6/3				
Pinus ponderosa				27/3	23/3	33/4	7/3	9/2			
Pinus washoensis				29/4	69/3	78/4	7/4	15/3			
Abies concolor				87/4	83/4[e]	72/4	100/5	100/5			
Pinus monticola								82/4			
Pinus contorta							19/3	6/3	78/4	7/3	7/3
Pinus albicaulis							6/1	12/2	91/4	100/6	100/5
Shrubs											
Rosa woodsii				21/3	20/2	11/3					
Amelanchier pallida			8/2	50/3	71/3	11/3	14/2	15/2			
Ribes viscosissimum				4/2		5/2	33/3	82/3			
Ribes cereum			13/2	17/2	11/3	28/2	7/2	3/1	4/3	6/2	7/1
Ribes montigenum		10/2	17/2	8/3	9/3	3/11	4/2	3/2	9/2	69/3	14/2
Artemisia tridentata	11/2	60/4	54/4	23/3	9/2	50/4	9/2	3/1	22/2	19/2	7/3
Symphoricarpos vaccinoides	11/1	50/3	75/3	38/3	3/2	50/3	78/3	64/2	50/2		
Herbs and grasses											
Veratrum californicum	100/6	20/3									
Heracleum lanatum	22/3										

TABLE 1. CONTINUED.

	(1) POTR/ VECA[b] P/C	(2) POTR/ ASFO P/C	(3) CELA/ BASA P/C	(4) ABCO/ LUCA P/C	(5) PIJE phase P/C	(6) PIWA phase P/C	(7) ABCO/ OSCH P/C	(8) ABCO/ PYPI P/C	(9) PIAL/ STCA P/C	(10) PIAL/ PEGR[c] P/C	(11) PIAL/ ARAC P/C
Deschampsia elongata	22/2										
Delphinium nuttallianum	50/3	11/2									
Ranunculus occidentalis	44/2	5/2									
Festuca ruba	25/4	22/3									
Nemophila breviflora	33/2	45/3	4/2								
Arabis divaricarpa	11/2	30/2	4/2				9/2				
Aster foliaceus	11/3	85/4									
Eriogonum umbellatum			33/3								
Balsamorhiza sagittata			58/4	23/2	35/2				4/3		
Mertensia oblongifolia	11/3	70/3	4/2	4/2	3/3	6/2					
Paeonia brownii		25/3	4/2	12/3	9/3	17/3					
Lupinus argenteus		20/5	8/3	13/3	12/4	17/2					
Eriophyllum lanatum		5/3	50/3	17/3	21/2	11/2					
Eriogonum nudum			29/2	10/3	12/3	6/2	1/3			6/3	
Erigeron inornatus			17/3	22/3	29/3	6/3					
Phacelia humilis		75/3	4/2	2/3		6/3	7/2			13/2	
Nemophila parviflora	40/2	22/2	8/2	2/2		6/2	4/2				
Polygonum douglasii		30/2		4/2	6/2		7/2				
Apocynum pumilum			4/2	31/4	47/4		4/2	3/2			
Cryptantha torreyana		35/2	13/2	6/2	9/2	28/2	4/2	6/2			
Elymus glaucus		10/3	29/3	22/3		32/3	16/3	3/1			
Hydrophyllum capitatum	56/2	60/3	4/1	12/2		33/2	29/3	12/2			
Chimaphila menziesii				2/3		6/3	3/2	45/2			
Castilleja applegatei		15/1	46/3	10/3	6/2	17/3	1/2	6/2			
Hieracium horridum		5/3	33/2	40/3	47/3	28/2	16/2	33/3			
Silene menziesii			8/2	25/3	18/4	39/2	17/3	12/3			

Table 1. Continued.

	(1) POTR/ VECA[b] P/C	(2) POTR/ ASFO P/C	(3) CELA/ BASA P/C	(4) ABCO/ LUCA P/C	(5) PIJE phase P/C	(6) PIWA phase P/C	(7) ABCO/ OSCH P/C	(8) ABCO/ PYPI P/C	(9) PIAL/ STCA P/C	(10) PIAL/ PEGR[c] P/C	(11) PIAL/ ARAC P/C
Smilacina racemosa			8/1	25/1	29/2	17/1	41/3	24/2			
Phacelia hastata			13/2	8/3	3/2	17/3	33/2	9/2			
Solidago canadensis				35/4	44/4	17/2	4/2	3/2			
Pterospora andromedea				23/2	29/2	11/3	6/2	42/2			
Calystegia polymorphus				22/3	24/3	17/4	1/2	3/2			
Hieracium albiflorum				15/3	12/3	12/3	39/3	48/3			
Potentilla glandulosa	11/3			22/2	24/2	17/2	14/2	6/2	17/2		
Phlox diffusa			58/3	8/2	3/3	17/2	3/1	3/2	22/3	6/2	
Collomia linearis	78/3	45/3	4/2	27/2	38/2	6/2	7/3	9/2			
Senecio aronicoides	11/2	60/3	33/3	19/2	15/2	28/2	13/3	3/2			
Osmorhiza occidentalis	35/2	56/2		4/2	6/2		1/2			6/2	
Vicia americana	56/3	65/4		54/3	56/3	50/3	39/3	18/3	4/4		
Thalictrum fendleri	44/2	45/1		6/2	3/2	11/2	39/2	13/2		19/1	
Achillea lanulosa	67/3	25/3	4/2	42/3	44/3	39/3		12/3	4/3	6/2	
Collinsia parviflora	33/3	65/3		12/3	12/3	11/2	26/3	6/2	17/3	6/4	
Osmorhiza chilensis			13/2	48/3	50/3	44/3	71/3	69/3	4/3	25/2	
Bromus marginatus	44/3	60/4	17/2	29/2	26/2	33/3	20/2	24/3		13/2	7/2
Agoseris glauca	56/2	30/3		19/2	15/2	22/2	1/2		52/3	25/3	14/3
Viola purpurea	22/2	65/3	29/2	17/2	15/2	22/2	61/3	9/2	13/2	50/3	7/2
Arenaria jamesiana	22/3	15/3	13/2	38/3	38/3	39/3	51/5	76/3	4/3	19/4	
Arnica cordifolia	5/4	5/4	17/2	52/3	15/2	11/3	25/4	73/3	4/2	38/4	14/2
Poa nervosa	5/2	15/3	25/2	10/3	3/3	22/3	12/3	42/2	65/3	63/3	29/3
Stipa californica		10/3	21/3	19/3	21/3	17/3	16/3	6/3	87/5	31/3	21/3
Stipa occidentalis		5/3	25/3	23/3	21/3	28/3	22/3	6/3	35/3	25/3	29/4
Lupinus caudatus		20/5	8/2	71/3	79/3	56/3	23/3	9/3		50/2	29/3
Penstemon gracilentus			8/2	4/2		11/2	36/3	33/2	30/3	75/2	21/2

TABLE 1. CONTINUED.

	(1) POTR/ VECA[b] P/C	(2) POTR/ ASFO P/C	(3) CELA/ BASA P/C	(4) ABCO/ LUCA P/C	(5) PIJE phase P/C	(6) PIWA phase P/C	(7) ABCO/ OSCH P/C	(8) ABCO/ PYPI P/C	(9) PIAL/ STCA P/C	(10) PIAL/ PEGR[c] P/C	(11) PIAL/ ARAC P/C
Arnica mollis				10/3	3/4	22/3	23/3	3/4	4/3		7/3
Pyrola picta				52/2	18/2	11/3	23/3	85/3		6/2	
Frasera speciosa	11/3						6/3	3/2	4/3	31/3	7/1
Synthyris missurica							4/2	33/2	19/2	13/2	14/2
Poa epilis							10/3		4/3	19/3	43/4
Trisetum spicatum							1/2	3/2	9/2	13/2	29/2
Calyptridium umbellatum									78/3	6/2	71/3
Helenium hoopesii									4/5	25/2	7/2
Arenaria aculeata			4/2						6/3		71/4
Arabis lyallii										19/2	29/2
Penstemon davidsonii										6/2	43/3

defined by linear combinations of the supplied environmental variables, including elevation, aspect, slope, and percent surface rock cover and topographic position (Gauch 1982).

Floristic relationships of the habitat types and phases are based on relative constancy and modal cover-abundance class of the definitive species found within a type or phase.

Results and Discussion

Four series, containing nine habitat types are recognized: *Cercocarpus ledifolius* (CELE), *Populus tremuloides* (POTR), *Abies concolor* (ABCO), and *Pinus albicaulis* (PIAL). One habitat type was further subdivided into phases.

Environmental data are presented by habitat type in Table 2. Means and ranges of height and cover for canopy, sapling, seedling, shrub, and herbaceous layers are presented in Table 3. Mean DBH and basal area are presented in Table 4.

Cercocarpus ledifolius (CELE) series. Cercocarpus is the dominant tree in a moderate canopy cover ($\bar{x}$ = 35%) with a moderate shrub ($\bar{x}$ = 25%) and moderate herbaceous cover ($\bar{x}$ = 35%). Basal area is typically low with small stem (2.5–12.2 cm) diameters. This series is found on exposed xeric upper slopes and ridges. Surface rock cover is variable, but is the highest in the study area. Soils are typically very rocky, shallow, and poorly developed. Litter depth is the lowest of all the series.

The *Cercocarpus ledifolius/Balsamorhiza sagittata* (CELE/BASA) habitat type typically occurs on southeast aspects and occupies the steepest slopes inhabited by forests. Sapling cover is primarily composed of *Cercocarpus* and secondarily of *Juniperus occidentalis. Cercocarpus* is the sole species in the seedling layer. *Symphoricarpos vaccinioides* and *Artemisia tridentata* dominate the shrub layer; *Balsamorhiza sagittata* dominates the herbaceous layer. Conspicuous herbs include *Phlox diffusa, Eriophyllum lanatum, Castilleja applegatei, Senecio aronicoides, Eriogonum umbellatum,* and *E. nudum.*

Vegetation dynamics. Cercocarpus ledifolius, a characteristic Great Basin xerophyte (Gleason and Cronquist 1964), is typically found growing on rocky, and immature soils. Oosting (1956) considered *C. ledifolius* to be a component within a climax community. According to Dealy (1975) this small tree (sometimes taking a shrub form) expands its populations from relict seed trees that are protected from fire on rocky sites. However, the oldest trees (1350 years) occur in the Shoshone Range of central Nevada between 2591–3049 m, in deep well developed soils on north to northeast aspects, below ridgelines, where snow accumulation provides soil moisture late into the growing season (Schultz 1987; Schultz et al. 1990). Typically the best developed stands are found on rocky sites protected from reoccurring fires as *C. ledifolius* is a weak sprouter (Wright et al. 1979). These sites may act as long-term refugia (Vasek and Thorne 1977).

Occasionally the CELE/BASA habitat type occurs on a small rocky island or rock bald with little or no soil, surrounded by entirely different vegetation. This type also can be found in areas of shallow soils within other forest types.

Populus tremuloides (POTR) series. Populus dominates the canopy and reproduction strata with moderate sized (7.7–42.7 cm) stems. Herbs dominate the vegetation under a variable tree canopy. Canopy cover ranges from open to dense (15–75%) with low shrub cover ($\bar{x}$ = 7%) and high herb cover ($\bar{x}$ = 76%). This series is commonly found on lower slopes with mesic to xeric conditions, on a broad variety of soils. Litter is relatively shallow.

The *Populus tremuloides/Veratrum californicum* (POTR/VECA) habitat type occurs on gentle slopes usually associated with seeps and streams with a western aspect. This type occurs in the most mesic areas of the study site. Soils are typically fine-textured, deep, and well developed. Surface soil moisture is evident throughout the growing season. Mean canopy cover of *Populus* is 33%. Sapling and seedling cover are moderate. *Symphoricarpos vaccinioides* and *Artemisia tridentata* are the only shrubs in this type, having a total mean cover of 1%. Herbaceous layer cover ($\bar{x}$ = 79%) is the highest of all types. *Veratrum californicum* dominates the understory. Other typical herbs include *Delphinium nutallianum, Ranunculus occidentalis, Festuca rubra,* and *Heracleum lanatum.*

The *Populus tremuloides/Aster foliaceus* (POTR/ASFO) habitat type occurs on gentle southeast facing slopes. Soils are typically coarse textured, moderately deep, and well developed. Mean canopy cover of *Populus* is 37%. *Symphoricarpos vaccinioides* and *Artemisia tridentata* dominate the patchy shrub layer with a total mean cover of 13%. Cover of the herbaceous layer is high ($\bar{x}$ = 72%), and is dominated by *Aster foliaceus.* On less disturbed and mesic sites *Mertensia oblongifolia* is common.

Vegetation dynamics. The biology of *Populus tremuloides* has been extensively examined (DeByle and Winokur 1985). Since *P. tremuloides* is a fast-growing and generally short-lived tree, most view it as seral when it is found in association with shade-tolerant conifers or long-lived hardwoods. However, when pure *P. tremuloides* stands are found without associate conifers, it is assumed to replace itself (Mueggler 1988). Such stands are all-aged and most likely developed from root suckering (Jones and DeByle 1985). Recently, DeByle et al. (1987) estimated that fire frequencies of 100 to 300 years are necessary to regenerate and maintain *P. tremuloides.*

Stands of POTR/VECA and POTR/ASFO were selected because

TABLE 2. ELEVATION, TOPOGRAPHY, SLOPE, ASPECT, SURFACE ROCK COVER, AND DEPTH OF FOREST FLOOR[a] BY FOREST HABITAT TYPE AND PHASE. [a]Depth of forest floor measures litter and decomposing organic matter above the soil's mineral layers.

	Elevation (m) mean / min–max	Topography mode / min–max	Slope (°) mean / min–max	Aspect mode / min–max	Surface rock cover % mean / min–max	Depth of forest floor (cm) mean / min–max
Cercocarpus ledifolius/Balsamorhiza sagittata type	2110 / 1739–2415	upper slope / ravine ridge	29 / 4–80	ESE / East–North	39 / 0–97	0.6 / 0–2.5
Populus tremuloides/Veratrum californicum type	2232 / 2101–2433	lower slope / near creek–upper slope	10 / 3–17	West / NE–WNW	14 / 0–55	0.8 / 0–3.8
Populus tremuloides/Aster foliaceus type	2200 / 2100–2396	lower slope / near creek–upper slope	11 / 2–26	ESE / ENE–WNW	14 / 0–95	0.8 / 0–5.1
Abies concolor/Lupinus caudatus type	1955 / 1780–2195	lower slope / near creek–ridge	16 / 1–44	West / NNE–North	11 / 0–65	5.3 / 1.3–15.2
Pinus jeffreyi phase	1889 / 1670–2149	lower slope / ravine–ridge	18 / 1–44	SW / NNE–North	10 / 0–65	5.1 / 1.3–15.2
Pinus washoensis phase	2082 / 1890–2195	lower slope / near creek–upper slope	14 / 2–36	North / ENE–N	18 / 0–55	5.3 / 1.3–12.7

TABLE 2. CONTINUED.

	Elevation (m) mean / min–max	Topography mode / min–max	Slope (°) mean / min–max	Aspect mode / min–max	Surface rock cover % mean / min–max	Depth of forest floor (cm) mean / min–max
Abies concolor/Osmorhiza chilensis type	2177 / 1878–2390	mid slope / near creek–ridge	17 / 2–40	West / NNE–N	8 / 0–60	6.1 / 1.2–14.0
Abies concolor/Pyrola picta type	2182 / 1829–2317	upper slope / near creek–upper slope	20 / 6–40	NNW / ENE–N	1 / 0–9	4.1 / 0.3–14.0
Pinus albicaulis/Stipa californica type	2525 / 2253–2720	upper slope / near creek–upper slope	14 / 3–26	West / East–North	6 / 0–45	1.8 / 0–7.6
Pinus albicaulis/Penstemon gracileutus type	2472 / 2329–2683	upper slope / mid-slope–ridge	22 / 5–47	NNE / NNE–North	8 / 0–40	2.8 / 0–7.6
Pinus albicaulis/Arenaria aculeata type	2665 / 2427–2979	ridge / upper slope–summit	22 / 2–36	NW / NNE–WSW	20 / 0–80	1.6 / 0–4.6

TABLE 3. CANOPY, SAPLING, SEEDLING, SHRUB, AND HERB COVER AND HEIGHT BY FOREST HABITAT TYPE AND PHASE.

	Canopy cover % mean / min–max	Height (m) mean / min–max	Sapling cover % mean / min–max	Height (m) mean / min–max	Seedling cover % mean / min–max	Shrub cover % mean / min–max	Height (m) mean / min–max	Herb cover % mean / min–max
Cercocarpus ledifolius/Balsamorhiza sagittata type	35 / 10–60	3.4 / 2.4–4.8	1 / 1–5	0–0.6 / 0.3–2.4	0.3 / 1–1	25 / 1–65	0.6 / 0.3–1.5	35 / 15–70
Populus tremuloides/Veratrum californicum type	33 / 15–65	10.7 / 5.5–18.3	8 / 0–75	0.9 / 0–2.7	3 / 0–7	1 / 0–5	0.6 / 0.3–0.6	79 / 13–97
Populus tremuloides/Aster foliaceus type	37 / 15–75	9.1 / 4.6–18.3	9 / 0–60	1.5 / 0–3.7	2 / 0–10	13 / 0–45	0.6 / 0–0.9	72 / 30–90
Abies concolor/Lupinus caudatus type	44 / 10–75	19.8 / 6.1–36.6	12 / 0–35	2.1 / 0–5.5	3 / 0–18	15 / 1–65	0.8 / 0.2–2.1	58 / 6–90
Pinus jeffreyi phase	46 / 10–70	20.1 / 6.1–33.5	12 / 3–35	2.1 / 0.9–3.7	2 / 0–7	11 / 1–40	0.8 / 0.3–2.1	60 / 6–88
Pinus washoensis phase	42 / 25–75	18.9 / 6.1–33.5	13 / 0–30	2.1 / 0–4.0	4 / 0–18	22 / 2–65	0.8 / 0.3–1.8	54 / 35–90
Abies concolor/Osmorhiza chilensis type	62 / 20–90	18.6 / 4.6–36.6	14 / 1–45	2.4 / 1.2–4.9	3 / 0–15	5 / 0–15	0.6 / 0–0.9	37 / 5–80

TABLE 3. CONTINUED.

	Canopy cover % mean / min–max	Height (m) mean / min–max	Sapling cover % mean / min–max	Height (m) mean / min–max	Seedling cover % mean / min–max	Shrub cover % mean / min–max	Height (m) mean / min–max	Herb cover % mean / min–max
Abies concolor/Pyrola picta type	56 / 15–90	22.0 / 6.1–36.6	28 / 2–90	2.7 / 1.5–3.7	4 / 1–10	8 / 0–40	0.6 / 0–0.9	35 / 5–90
Pinus albicaulis/Stipa californica type	46 / 20–80	11.3 / 6.1–18.3	14 / 3–45	2.7 / 0.9–3.7	4 / 0–35	1 / 0–15	0.2 / 0–0.9	58 / 20–85
Pinus albicaulis/Penstemon gracilentus type	49 / 15–80	9.1 / 3.4–18.3	7 / 2–25	1.8 / 0.6–3.0	1 / 1–5	10 / 0–50	0.6 / 0–0.9	32 / 15–70
Pinus albicaulis/Arenaria aculeata type	31 / 8–50	6.4 / 3.0–13.7	10 / 3–40	1.8 / 0.6–3.7	2 / 0–5	1 / 0–8	0.2 / 0–0.6	49 / 3–80

TABLE 4. BASAL AREA (m^2 ha^{-1}) AND STEM DBH (cm) BY SPECIES FOR *CERCOCARPUS LEDIFOLIUS*, *POPULUS TREMULOIDES*, *ABIES CONCOLOR* AND *PINUS ALBICAULIS* SERIES.

Series/species	Basal area mean/SD		DBH mean/SD range	
	Live	Dead	Live	Dead
Cercocarpus ledifolius (n = 65 live) (n = 13 dead)	33.67/7.01	7.65/7.01	7.12/2.33 2.5–12.2	4.33/1.79 2.0–8.3
Populus tremuloides (n = 29 live) (n = 2 dead)	48.21/3.25	4.59/6.49	25.1/7.69 7.7–42.7	24.0/9.0 17.0–31.0
Abies concolor (n = 32 live) (n = 2 dead)	74.61/14.21	6.89/2.65	21.61/15.09 5.5–75.0	16.35/10.12 9.2–23.5
Pinus albicaulis (n = 31 live) (n = 9 dead)	33.67/10.60	18.37/12.15	23.59/14.29 4.9–57.3	30.41/15.21 8.2–60.8

they lack coniferous associates; however, some stands in the South Warner Mountains have *Abies concolor* and sometimes *Pinus* associates, particularly *P. contorta.* These stands are probably seral to ABCO series types. However, the suppression of fire and heavy grazing, characteristically associated with the POTR/ASFO, may favor the establishment of *A. concolor* and *P. contorta* (Mueggler 1985).

Heavy grazing probably has contributed to the abundance of *Veratrum californicum* in the POTR/VECA habitat type (Mueggler 1988). It is interesting to note that *Draba stenoloba* var. *ramosa* is almost exclusively found in the understory of *Veratrum,* suggesting a soil moisture and/or shade requirement. The abundance of *Aster foliaceus* and other forbs in the POTR/ASFO habitat type is also a probable response to cattle grazing (C. G. Johnson, Jr., pers. comm., Nov 1989).

Abies concolor (ABCO) series. Abies is the dominant species in the reproduction strata. Canopy cover varies from open to dense (10–90%) with low shrub ($\bar{x}$ = 9%) and moderate herb cover ($\bar{x}$ = 43%). Basal area is the highest of all series described, a function of many suppressed *Abies* growing beneath the canopy of large, older *Pinus* and *Abies* (5.5–75.0 cm). This series occupies more area and has the largest elevation range of all the series. It occurs from lower to upper slopes and is also found near creeks and on ridges. Soils are coarse textured, well drained, and moderately to highly developed. Litter is the deepest of all the series.

The *Abies concolor/Lupinus caudatus* (ABCO/LUCA) habitat type commonly occurs on lower west slopes but does range from creek side to ridges. Overstory is generally open but cover is quite variable (10–75%). *Pinus jeffreyi* dominates with lesser amounts of *Abies. Pinus washoensis* and *P. ponderosa* are associates with nearly equal constancy but with relatively low covers. *Abies* constitutes the majority of the regeneration in the sapling and seedling layers. Shrub cover is moderate ($\bar{x}$ = 15%), often characterized by *Amelanchier pallida.* The herbaceous layer, dominated by *Lupinus caudatus,* has a moderately high cover ($\bar{x}$ = 58%). Herbs definitive of this type include *Hieracium horridum, Solidago canadensis, Apocynum pumilum,* and *Silene menziesii.*

There are two phases within the ABCO/LUCA type: *Pinus jeffreyi* (PIJE) phase and *P. washoensis* (PIWA) phase. Though the shrub and herbaceous taxa are similar in the phases, their frequency and cover is greater in the *Pinus jeffreyi* phase.

The *Pinus jeffreyi* phase inhabits the lower to mid elevations 1670–2149 m on lower southwest slopes. Canopy cover averages 46%, with *Pinus jeffreyi* and *Abies* common. The sapling and seedling layers are mostly *Abies* and *Pinus jeffreyi.*

Conversely, the *Pinus washoensis* phase inhabits mid to upper elevations 1890–2195 m on north aspects. Mean canopy cover is 42% of mainly *Pinus washoensis* and *Abies*. *Abies* dominates the sapling and seedling strata.

The *Abies concolor/Osmorhiza chilensis* (ABCO/OSCH) habitat type characteristically occurs on midslopes on west aspects but can be found from creek to ridges. Canopy cover varies but has the highest mean cover (62%) of all types described. *Abies* is the dominant canopy tree. *Pinus albicaulis* is a higher elevation associate, whereas *P. washoensis, P. jeffreyi,* and *P. ponderosa* occur at mid- to lower elevations. *Abies* dominates reproduction in the sapling and seedling layers. Shrub cover is low ($\bar{x}$ = 5%) with *Symphoricarpos vaccinioides* comprising half of the shrub layer. A moderate herbaceous cover ($\bar{x}$ = 37%) is dominated by *Osmorhiza chilensis*. Other taxa characteristic of this type are *Smilacina racemosa* and *Phacelia hastata*.

The *Abies concolor/Pyrola picta* (ABCO/PYPI) habitat type characteristically occurs on upper northwesterly facing slopes. Mean canopy cover is 56%. *Abies* is the canopy dominant, and *Pinus monticola* a codominant. Other associated trees include *P. washoensis, P. albicaulis, P. ponderosa,* and *P. contorta*. Sapling cover ($\bar{x}$ = 28%) is by far the highest of all the types. Mean cover of the shrub and herb layers are 8% and 35%, respectively. *Ribes viscosissimum* dominates the sparse shrub layer, *Pyrola picta* the herb layer. Other common herbs are *Arenaria jamesiana, Arnica cordifolia, Osmorhiza chilensis,* and *Hieracium albiflorum*.

Vegetation dynamics. Abies concolor reproduction is reduced in areas where lightning-caused fires are fairly frequent (U.S.D.A. 1965; Vale 1977). With fire suppression, *A. concolor* increases with a concurrent decrease in *Pinus* reproduction which together can result in a gradual change in structure and composition in ABCO/LUCA and ABCO/PYPI.

Overgrazing in *Artemisia tridentata*-steppe communities was responsible for the invasion and establishment of *A. concolor* trees (Vale 1975, 1977). Such invasion may account for the unusually xeric *A. concolor* stands and extent of ABCO/OSCH.

Lupinus caudatus, a palatable plant but poisonous to cattle and horses, is abundant in ABCO/LUCA. Its abundance may be a response to previous overgrazing (Hopkins 1979).

The Pinus complex of the ABCO/LUCA type. The ABCO/LUCA type is characterized by the occurrence of three diploxylon pines: *Pinus jeffreyi, P. ponderosa,* and *P. washoensis* all well studied in the area (Haller 1961, 1965; Smith 1967, 1971, 1981; Critchfield and Allenbaugh 1969; Griffin and Critchfield 1972; Critchfield 1984). The genetic, taxonomic, and ecological relationships of the pines in northeastern California are complicated because *P. jeffreyi* and "good" *P. washoensis* reach their northeastern range limits here (Critchfield 1984; J.R. Haller pers. comm., July 1978). Also, the geographical-morphological transition from the more typical race of Pacific *P. ponderosa* to the North Plateau races of northeastern California to British Columbia and Montana occurs in this general area (Critchfield, 1984; J. R. Haller pers. comm., July 1978).

In contrast to Haller's (1961) observations, we found that *P. jeffreyi* has a greater elevation range within the Wilderness Area than *P. ponderosa* and *P. washoensis.* There are few pure stands, however, of *P. jeffreyi* within the area, which is probably because purer, lower elevation stands do not occur within the elevation range (1457 m) of the wilderness boundary. "Good" individual representatives of *P. jeffreyi* are rare and occur on exposed xeric sites at approximately 2238 m. The lower elevation *P. jeffreyi* presented no problem in identification, but, at mid-elevations (1921–2043 m), *P. ponderosa* appeared quite varied with many possible intermediates with *P. washoensis.* The majority of *P. washoensis* was found as a codominant, in the lower to mid elevation (1890–2195 m) ABCO/OSCH type. At higher elevations (2043–2195 m), *P. washoensis* was the dominant pine.

Pinus albicaulis (PIAL) series. Pinus albicaulis dominates or shares the dominance of the canopy, sapling and seedling layers with *P. contorta.* Canopy cover generally is moderately open ($\bar{x}$ = 42%), with low shrub ($\bar{x}$ = 4%) and moderate herb ($\bar{x}$ = 46%) cover. Basal area is low with considerable variation in stem diameters (4.9–57.3 cm). This series is found from upper slopes to summits. Soils are typically coarse textured, excessively drained and poorly developed. Surface rock cover is highly variable. Litter depth is typically shallow.

The *Pinus albicaulis/Stipa californica* (PIAL/STCA) habitat type typically inhabits upper slopes on western aspects, but can also be found near streams or springs. Canopy cover is moderate ($\bar{x}$ = 46%); however, *Pinus albicaulis* and *P. contorta* cover is highly variable. In the sapling layer both occur with equal constancies, but with a lower cover than in the canopy. *Symphoricarpos vaccinioides* dominates the sparse cover ($\bar{x}$ = 1%) of the shrub layer. The herb layer has moderately high mean cover of 58% and is dominated by *Stipa californica.* Important herbs are *Calyptridium umbellatum, Poa nervosa, Agoseris glauca, Stipa occidentalis,* and *Phlox diffusa.*

The *Pinus albicaulis/Penstemon gracilentus* (PIAL/PEGR) habitat type commonly inhabits upper northeast facing slopes, but also occurs on high ridges. Canopy cover is moderate ($\bar{x}$ = 49%). *Pinus albicaulis* is the dominant and *P. contorta* is an infrequent associate. Sapling and seedling cover is low with similar proportions. Shrub cover is sparse ($\bar{x}$ = 1%) with *Ribes montigenum* the dominant. Herb cover is moderate ($\bar{x}$ = 32%) but highly variable. Taxa descriptive of this type are *Penstemon gracilentus, Poa nervosa, Frasera speciosa,* and *Anemone drummondii.*

The *Pinus albicaulis/Arenaria aculeata* (PIAL/ARAC) habitat type characteristically occurs on upper northwest facing slopes to the summits where some trees form krummholz. Canopy over ($\bar{x}$ = 31%) is the sparsest within the study. *Pinus albicaulis* dominates both the canopy and sapling strata. *Pinus contorta* occurs as an infrequent associate at the lower elevations within this type. *Ribes montigenum* and *Haplopappus bloomeri* dominate the sparse cover ($\bar{x}$ = 1%) shrub layer. *Arenaria aculeata* dominates a moderate cover ($\bar{x}$ = 49%) herb layer. Important herbs are *Penstemon davidsonii, Arabis lyallii, Trisetum spicatum, Raillardella argentea, Castilleja arachnoidea,* and *Senecio fremontii.*

Vegetation dynamics. Within PIAL/STCA, *Pinus albicaulis* and *P. contorta* appear to reproduce with near equal frequencies. Despite Vale's (1977) prediction that *P. contorta* is decreasing and *P. albicaulis* is increasing because of lack of fire, our data suggest that both are successfully reproducing and are persistent. *Pinus albicaulis* is also more drought and cold tolerant than *P. contorta* (Parsons 1980; Arno and Hoff 1989).

Above 2713 m, *Pinus albicaulis* is the canopy and reproductive dominant whereas *P. contorta* is only occasional. Our observations of fire-scarred trees and pieces of charcoal on the soil surface suggest an increase of fire with increasing elevation. The structure of the higher elevation stands does not favor rapid spread of ground fires. Higher elevation lightning-caused fires usually self-extinguish for lack of fuel. Other reasons seem better to explain the decreasing numbers of *P. contorta* with increasing elevations. It may be that the wider ecological amplitude of *P. albicaulis* allows it to increase in dominance in subalpine environments (Rundel et al. 1977; Arno and Hammerly 1984; Arno and Hoff 1989).

An alpine zone has been indicated for the South Warner Mountains (Major and Taylor 1977). Tree limit of *Pinus albicaulis* does not exist on any summit, including Eagle Peak, the highest in the Warner Mountains. Both flagged krummholz and cushion krummholz (Arno and Hammerly 1984) trees occur on very exposed and rocky sites, usually in the protection of large rocks, but, more commonly, stunted trees 1.8–3 m in height occur near the summits.

The summits along the crest of the South Warner Mountains provide habitat for many species known from the alpine zone in California (Munz 1973; Major and Taylor 1977), including *Arabis lemonii, A. lyallii, Calyptridium umbellatum, Oxyria digyna, Castilleja arachnoidea, Penstemon davidsonii, Ivesia gordonii, Lupinus lyallii, Senecio fremontii,* and *Raillardella argentea.* Few of these species are restricted to alpine environments, but instead are typical of subalpine and even open montane habitats. Hence, both forest structure and species composition of the summit area of Eagle Peak indicate a subalpine, not alpine, vegetation.

Vegetation pattern and the environment. Inferred environmental variables were analyzed with direct gradient and principal component analyses (Fig. 1). Habitat types occur along elevation and soil moisture gradients. POTR/VECA is proximate to seeps, springs, and streams. POTR/ASFO occurs from moderately mesic to superficially xeric sites. Both types appear to be associated with subirrigated soils at a wide range of elevations. CELE/BASA is associated with dry and poorly developed soils. ABCO and PIAL habitat types are found along a well-defined elevation, soil moisture gradient. Hence, CELE and POTR are primarily edaphically controlled, whereas the coniferous forest types are more influenced by environmental variables that change with elevation.

The orographic effect also affects the patterning of vegetation. Forests on the gentle west slope are more extensive than those of the steeper, rockier east slope. However, floristic composition and environmental variables were found to be equivalent for the purpose of classification.

Relationship to other vegetation types. The forest vegetation in the South Warner Mountains is most similar floristically and ecologically to the North Warner Mountains in Oregon. Hopkins (1979) described two plant associations that are restricted to the North Warner Mountains in Oregon. His white fir-ponderosa pine-western white pine/sticky currant (*Ribes viscosissimum*) association is similar to our ABCO/PYPI habitat type. Both are found strictly on northerly aspects on mid- to upper slopes within similar elevation ranges. Hopkins's (1979) lodgepole pine-whitebark pine-western white pine/sandwort (*Arenaria kingii*) association resembles our PIAL/STCA habitat type except for the absence of *Abies concolor, Pinus monticola,* and *Arctostaphylos nevadensis.* Other vegetation classifications in central and southeastern Oregon have described forest types that are similar to our habitat types (Franklin and Dyrness 1973; Hopkins 1979; Volland 1976). Though overstory conifer composition may be different, understory vegetation is strikingly similar.

Smith et al. (1988) described four forest ecological types that occur in the Warner Mountains of California. Two are restricted by soil type and landform north of Cedar Pass. On Buck Mountain, the *Pinus washoensis/Arctostaphylos nevadensis/Poa nervosa* type occurs on soils derived from rhyolite and obsidian and is comprised solely of *P. washoensis.* Near Lassen Creek, the *Pinus ponderosa/Amelanchier pallida-Ceanothus velutinus/Arnica cordifolia* type is found only on scarps and is solely comprised of *P. ponderosa.* South

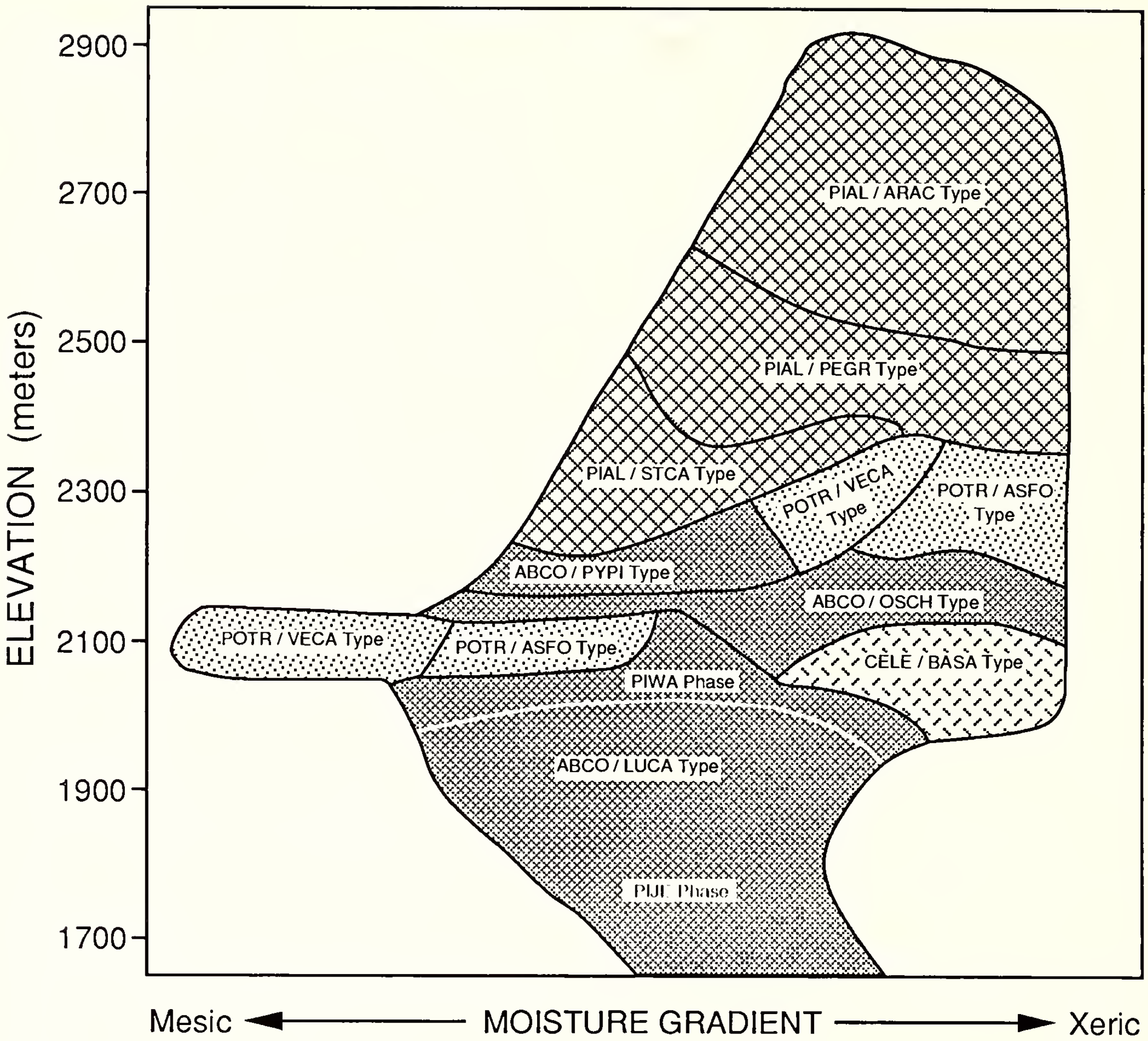

FIG. 1 Approximate distribution of South Warner Mountains forest habitat types along soil moisture and elevation gradients incorporating a principal component analysis and direct gradient analysis. Abbreviations equal the following type and phase names: *Cercocarpus ledifolius/Balsamorhiza sagittata* (CELE/BASA) type, *Populus tremuloides/Veratrum californicum* (POTR/VECA) type, *Populus tremuloides/Aster foliaceus* (POTR/ASFO) type, *Abies concolor/Lupinus caudatus* (ABCO/LUCA) type, *Pinus jeffreyi* (PIJE) phase, *Pinus washoensis* (PIWA) phase, *Abies concolor/Osmorhiza chilensis* (ABCO/OSCH) type, *Abies concolor/Pyrola picta* (ABCO/PYPI) type, *Pinus albicaulis/Stipa californica* (PIAL/STCA) type, *Pinus albicaulis/Penstemon gracilentus* (PIAL/PEGR) type, and *Pinus albicaulis/Arenaria aculeata* (PIAL/ARAC) type. The empty area represents types that do not exist or are unsampled.

of Cedar Pass, the *Pinus washoensis/Symphoricarpos vaccinioides/Bromus orcuttianus* type is found on soil derived from basalt. Our PIWA phase of the ABCO/LUCA habitat type is an extension in geographical area of the latter type. The fourth type, *Pinus ponderosa-Abies concolor/Amelanchier pallida/Poa nervosa,* is found scattered throughout the west side of the northern Warner Mountains and appears very similar to our ABCO/LUCA habitat type. *Pinus jeffreyi* and *P. washoensis* are absent from their type whereas *Arctostaphylos nevadensis* is absent from ours.

The PIJE phase within the ABCO/LUCA habitat type is similar to vegetation described by Vasek (1978) in *Pinus jeffreyi* stands in southwestern Modoc Co. Differences include lower cover of *A. concolor* in Vasek's sites and the absence of *Calocedrus decurrens* in the southern Warner Mountains.

In the Whitehorse Mountains, near the Nevada border of southeastern Oregon, Dealy (1975) described a *Balsamorhiza sagittata* phase within a *Cercocarpus ledifolius/Symphoricarpos oreophilus* community that has both environmental and floristic similarities to our CELE/BASA habitat type. POTR/VECA communities have been described on deep, moist, poorly drained soils in the Uinta Mountains, Wasatch Range, and San Pitch Mountains of Utah (Mueggler 1988), in the Santa Rosa, Independence, and Jarbridge ranges in northern Nevada (Mueggler 1988), and in northwestern Colorado (Hoffman and Alexander 1980).

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NOTEWORTHY COLLECTIONS

CALIFORNIA

MALOSMA LAURINA (Nutt. in Torrey & A. Gray) Nutt. ex Abrams (ANACARDIACEAE).—San Luis Obispo Co., outskirts of Arroyo Grande, hills on W side of Oak Park Rd, ca. 0.5 km N from jctn with Noyes Rd, population of ca. 20 shrubs in *Quercus agrifolia* woodland, 16 Mar 1990, *D. Keil 21343 with L. D. Oyler* (OBI); large shrubs scattered in coastal scrub and chaparral on hills E of Hwy 227, N of Arroyo Grande, ca. 0.5 km S from jctn with Noyes Rd, 20 Mar 1990, *D. Keil 21346 with V. L. Holland* (OBI).

Previous knowledge. Coastal hills and mountains along Pacific slope from Santa Ynez Mts. of Santa Barbara Co., California to middle of Baja California peninsula (Munz, *A California Flora,* 1959; Smith, *Flora of the Santa Barbara region, California,* 1976; Wiggins, *Flora of Baja California,* 1980).

Significance. First records for San Luis Obispo Co., a northward range extension of ca. 70 km. *Rhus integrifolia* Nutt., similarly disjunct from Santa Barbara Co., was present in chaparral on the site where *Keil 21346* was collected. Keil et al. (Madroño 32:214–224, 1985) reported *R. integrifolia* as new to San Luis Obispo County from a site ca. 0.5 km N of this location.

Smith (l.c.) noted that *M. laurina* is frequently planted along highways in Santa Barbara County. Human introduction of *M. laurina* into San Luis Obispo County cannot be ruled out; species exotic to the site (e.g., *Eucalyptus globulus* and *Pinus radiata*) are well-established in areas near the site for *Keil 21346.* In any case *M. laurina* is well established and reproducing in the Arroyo Grande area.—DAVID J. KEIL, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.